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ARE THERE FOLIAR GAPS IN THE LYCOPSIDA?[1]

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(WITH PLATES XVII AND XVIII)

Six years ago the present writer published an account of his studies on the stem of the pteridophytes and gymnosperms.[2] In the conclusions not only these large groups were considered, but also the remaining vascular plants, which had been the subject of earlier investigations. The general result was reached "that there are two phylogenetic types of tubular central cylinder, namely, that in which only ramular gaps are present, and that in which both ramular and foliar gaps occur." Further it was stated: "The use of these constant and characteristic anatomical features results in the division of the Vasculares into two great primitive stocks—the Lycopsida, which are cladosiphonic and palingenetically microphyllous, and the Pteropsida, which are phyllosiphonic and palingenetically megaphyllous. The Lycopsida include the Lycopodiales and Equisetales. The Pteropsida include the Filicales, Gymnospermae, and Angiospermae." The opinion was expressed that the Lycopsida and Pteropsida "appear to have been separate back to the beginning of the period when the paleontological record begins." Since the publication of that memoir, the writer has been busily engaged in other directions, and his time has been fully taken up. In the interval a great deal of literature has appeared, especially in European countries, on the anatomy and phylogeny of vascular plants, and not unnaturally the writer's hypothesis has been subjected to the criticism which is the fate of every scientific hypothesis. The most vigorous objections to

[1] Contributions from the Phanerogamic Laboratories of Harvard University, No. 14.

[2] Phil. Trans. Roy. Soc. London B. 195:119–146. 1902.

the hypothesis, as might be expected, have been raised by those whose published views are prejudicially affected by its validity. In spite of all that has been written on the subject, however, the author has seen no reason to modify his standpoint in any essential feature. It is proposed in the present article to deal with some of the objections, mainly resulting from a misapprehension of the author's statements or an unfamiliarity with the anatomical field, which have been raised against the Lycopsida. In a subsequent article the Pteropsida will receive consideration.

It will perhaps be well at the beginning to define the Lycopsida and Pteropsida in a comprehensive way and to include external characters as well as anatomical ones.

LYCOPSIDA.—Palingenetically microphyllous vascular plants, with ventrisporangiate sporophylls (sporangia adaxial), the tubular central cylinder when present characterized by the entire absence of gaps or interruptions in the fibrovascular tissue immediately above the outgoing leaf-traces.—Lycopodiales, Psilotales, Equisetales, Sphenophyllales.

PTEROPSIDA.—Palingenetically megaphyllous vascular plants, with dorsisporangiate sporophylls (sporangia abaxial), the tubular central cylinder when present characterized by foliar gaps or interruptions in the fibrovascular tissues immediately above the outgoing foliar traces.—Filicales, Gymnospermae, Angiospermae.

It is necessary to define very clearly, on account of numerous misconceptions and misunderstandings, the nature of a foliar gap, for the writer's critics have shown considerable versatility of misunderstanding in regard to this important feature. In one of the more simply organized ferns (Ophioglossum, Osmunda, Schizaea, Mohria, Adiantum, etc.), wherever a leaf passes off from the surface of the stem, it carries with it a fibrovascular strand, the leaf-trace. The foliar trace is derived from the tubular central cylinder of the stem, and as it bends away from the surface of the stele in its outward and upward course, it causes immediately above it, in the stelar wall, an interruption of the fibrovascular tissues, known as the leaf gap. The foliar gap may be distinguished from other gaps in the wall of the fibrovascular hollow cylinder by the fact that it occurs immediately above a leaf-trace. A true foliar gap, moreover, is always

related to but a single leaf-trace. If several traces appear in relation to a stelar gap, and especially if they are related to the *sides* of the gap, it may be concluded at once that no true foliar gap is present. It may be added for the benefit of inexperienced anatomists that not all gaps in the wall of the central cylinder are foliar gaps. Where the fibrovascular tissues are much reduced in amount, as is not unfrequently the case, they often break up into a loose meshwork, which has no necessary relation to the vascular supply of the leaves or the branches.

Lepidodendreae and Sigillariae

In the memoir cited above, the writer has called attention to the fact that in the Lepidodendreae, which are among the oldest of the Lycopsida, there are no foliar gaps in the tubular central cylinder, when present. *Fig. 9* illustrates this feature in *Lepidophloios Harcourti*. Below in the figure is to be seen the woody cylinder, showing inferiorly some of the thin-walled tissue of the pith. The cylinder is dentate on its outer surface, and the teeth are composed to some extent of small-celled protoxylem. Outside the wood may be seen nests of small cells, which mainly lie in the intervals between the dentations. These are the foliar traces. It is clear that there are no gaps or interruptions in the central cylinder corresponding to these. Consequently it may be stated that there are no foliar gaps in the species figured. An examination of a considerable number of sections of lepidodendrid stems has made it clear that foliar gaps are absent in the group.

In the older Sigillariae the primary wood in the stem ordinarily formed a continuous cylinder, and there were, as in Lepidodendron, no gaps of any kind except for the outgoing strands of branches. In more modern Sigillarias, however, the woody cylinder was frequently entirely or partially broken up into separate strands. *Sigillaria elegans* from the Lower Coal Measures had the continuous type of woody cylinder, while *S. Menardi* from the Permian had separate strands of wood constituting its tubular stele.[3] The leaf-traces in both types of Sigillaria stem, however, passed off without leaving any foliar gaps in the central cylinder, for in the Sigillarias of the more

[3] Kidston, R. Internal structure of *Sigillaria elegans*. Trans. Roy. Soc. Edinburgh **41**:533–550. 1905.

modern type, with the cylinder broken up into numerous bundles, the gaps between the strands were not subtended by the leaf-traces, which took their origin from the face of the fibrovascular bundles. This fact it is very important to keep in mind, in view of the conditions to be found in some of the reduced Lycopsida to be described later. It is further of interest to note that these arboreous lycopods, in which the leaves were sometimes a meter in length, offer no exception in their anatomical structure to the writer's definition of the Lycopsida.

LYCOPODIACEAE

Under this heading Lycopodium itself need not be considered, as it has a solid protostelic central cylinder. Phylloglossum, however, has a tubular stele, which in the lower tuberous portion of the stem constitutes in cross-section an almost continuous horseshoe of xylem, without foliar gaps for the relatively large radical leaves (protophylls). The opening in the horseshoe corresponds to the outgoing strand which passes into the resting tuber, forming the next year's plant. Above the tuber the stem of Phylloglossum passes into the slender peduncle of the cone. In this region of the stem the fibrovascular tissues separate into a number of distinct strands, comparable to those found in the axis of the less ancient Sigillarias. *Fig. 8* is a copy of a figure by BERTRAND,[4] showing the manner in which these isolated peduncular strands give rise to the traces of the lower sporophylls of the cone. It will be noted on the lower side of the figure that the bundles are much elongated radially. In such cases they are about to give off sporophyll traces. In the upper part of the figure three outgoing traces are seen, in different degrees of detachment from their corresponding peduncular strands. On the left, one of the traces has turned obliquely after leaving the peduncular strand, so that it nearly subtends the hiatus between two peduncular strands. An inattentive observer might readily interpret the hiatus as a real foliar gap. Only a consideration of the mode of origin of the trace from the peduncular strand makes the real condition of affairs apparent. There are clearly no foliar gaps present, else the peduncular strands would fork above the outgoing traces. The conditions in the upper part of the stem of Phylloglossum are clearly similar to those obtain-

[4] Phylloglossum. Archives Bot. du Nord de la France **1885**: 112. *fig. 102.*

ing in a Sigillaria with separate fibrovascular strands. In the cone of Phylloglossum individual sections often present an appearance still more misleading. In *fig. 10* is shown such a condition. A horse-shoe-shaped fibrovascular mass appears in the center, and opposite its opening a sporophyll trace. To the right and left below are two other foliar traces. An inexperienced anatomist might readily conclude that the gap opposite the uppermost trace was a true foliar gap. *Fig. 11* shows a section from another cone, with two such apparent foliar gaps, one on each side, each apparently subtended by its corresponding leaf-trace. *Fig. 12* shows another section from the same cone, a small fraction of a millimeter lower down. It is here to be noted that the foliar trace on the right in the preceding figure joins the *face* of the large cauline fibrovascular strand, forming the same radially elongated mass as is characteristic of the outgoing sporophyll traces shown in *fig. 8* from the peduncle. Still lower down, as was learned from the study of serial sections, the foliar strand on the left joined the outside of its cauline strand in a similar manner. A study of the cone of Phylloglossum has shown that the traces for the sporophylls invariably pass off from the outer surface of the central cylinder without leaving any real foliar gaps. Sometimes two or even three traces may originate along the margins of the same hiatus in the stele. The interruptions in the central cylinder or stele are no more to be regarded as foliar gaps than are the corresponding ones in certain Sigillarias. It is obviously impossible with any clear eye to anatomical relations to regard the perforations which exist in the upper part of the fibrovascular system of the stem in Phylloglossum as being of the nature of foliar gaps. Miss SYKES has recently reached the conclusion that the living Lycopodiaceae originated in all probability by reduction from the more complex arboreous lycopods of the Paleozoic period.[5] Without presuming to indorse this view, it may be pointed out that it stands in the way of presumably reduced modern lycopodineous forms in any case possessing the foliar gaps which were denied to their supposed Paleozoic ancestors, which possessed very much larger leaves.

[5] Morphology of the sporangium-bearing organs in the Lycopodiaceae. New Phytologist 7:41–60. 1908.

PSILOTACEAE

Fig. 6 shows a magnified view of the stem of *Tmesipteris tannensis*, as viewed in transverse section. On the lower left side is a blunt projection from the surface of the stem, the base of a sporophyll.[6] At the top of the figure is another sharper projection, which is the basal portion of a foliage leaf. Subtending each of the projections from the surface of the stem noted above is a fibrovascular strand, which has recently come off from the central cylinder. *Fig. 7* shows part of the foregoing more highly magnified, to make clear the relations of the outgoing traces to the stele of the stem. With the greater magnification an additional trace can be seen emerging from the central cylinder on the lower right hand. In passing out none of these three traces subtends a gap in the central cylinder, which in this region is a continuous fibrovascular tube. In the upper region of the stem, particularly where it gives rise to sporophylls, as BERTRAND has pointed out,[7] the central cylinder breaks up into separate strands, much as happens in the upper part of the axis of Phylloglossum. In isolated transverse sections one often sees appearances such as are represented in *figs. 10* and *11* of the present article. On the strength of such evidence Miss SYKES[8] has asserted that there are foliar gaps in Tmesipteris. Her own figures, however, cannot be reconciled with this statement. On page 71 she represents sections taken at various heights through a portion of the stem, and makes a diagram of the bundle arrangement in this region. According to her figures the gaps are mainly on one side of the central cylinder or stele, and no less than three traces are related to one of these, that is, they are derived from the fibrovascular strands along its *lateral* margins. Three other traces originate near smaller stelar lacunae and one comes off remote from any gap. A greater inconstancy in the mode of origin of traces could scarcely be imagined. A general acquaintance with fibrovascular anatomy should make it clear that true foliar gaps in the same region of the stem should be nearly of a size and should occur immediately *above a single* leaf-trace. This state of affairs is

[6] Miss SYKES prefers to regard this as a *fertile branch.*

[7] Recherches sur les Tmesipteridées. Archiv. Bot. du Nord de la France **30**:—. 1882.

[8] Anatomy and morphology of Tmesipteris. Annals of Botany **22**:63–89. 1908.

very far from being realized in Tmesipteris as described by Miss SYKES. The conditions are in fact the same as those found in the corresponding region of the stem in Phylloglossum. Miss SYKES has been so good as to loan her sections, and the series, although not complete, vouch for the general accuracy of her figures. One fact of importance appears, however, to have escaped her notice, although it is clearly indicated in the sections, namely, that in every case the outgoing strands of appendages originated *opposite* the strands of the central cylinder and did not subtend any gap *at their point of origin*, although some of them by a subsequent oblique course, as in Phylloglossum, seemed to subtend the stelar gaps. Appearances of this kind have been brought to the attention of Professor BOWER, and he figures one such section on page 420 and again on page 487 of his recent work.[9] He expresses the opinion that his figure overthrows the hypothesis of JEFFREY on the lycopsid side. He further adds in a footnote: "The Botryopterideae are not phyllosiphonic; thus the anatomical distinction of JEFFREY breaks down on both sides." In this added statement he is even less happy than in the original one, for he is apparently unaware that ferns with a protostelic central cylinder cannot possibly be phyllosiphonic, that is, possess foliar gaps. In all of the Botryopterideae in which the origin of the foliar strands has yet been described the central cylinder is protostelic. Professor BOWER is in general not entirely at home in discussing anatomical facts. As a further example of this, may be cited his statement that *Alsophila excelsa*, as described by GWYNNE-VAUGHAN, shows a "transition from the cladosiphonic to the phyllosiphonic" condition in the young plant. Professor TANSLEY in a review of Professor BOWER'S book[10] very properly criticizes this singular misunderstanding in the following words: "Mr. GWYNNE-VAUGHAN will be probably surprised to learn that he has shown a 'transition from the cladosiphonic to the phyllosiphonic' state in *Alsophila excelsa*. What really exists, of course, is a transition from protostely to siphonostely, and protostely is not a monopoly of the microphyllous forms, but is found equally among the primitive ferns." It cannot be too strongly emphasized that, especially in difficult cases,

[9] The origin of a land flora. London. 1908.

[10] New Phytologist **7**:126. 1908.

like those occurring in the reduced Lycopsida, thin serial sections are necessary to a proper understanding of the real anatomical relations. It may be stated in conclusion that there are no real foliar gaps in Tmesipteris and that statements as to their presence depend on errors of observation and interpretation.

In Psilotum leaf-traces are absent in the case of the vegetative leaves, but as the angles of the stellate central cylinder subtend the ridges of the stem from which the leaves take their origin, there can be no question of the presence of foliar lacunae in this genus. Traces are present in the case of the sporophylls, but as these in general occur on the smaller terminal branches, where the stele is solid, they do not serve to elucidate the subject. It is of particular interest that the leaf-traces should sometimes disappear altogether in the case of the small-leaved forms (the Lycopsida). The writer has called attention to this condition as occurring in the case of the basal foliar sheaths of the smaller branches of Equisetum.[11]

EQUISETALES

It is in regard to the supposed existence of foliar gaps in the equisetal series that the writer has received the most weighty criticism. Dr. SCOTT in his masterly treatment of Paleozoic botany in *Progressus rei botanicae*, adopting the present author's division of vascular plants into two phyla, the Lycopsida and Pteropsida, states that it is "open to much criticism; the general grouping however has sufficient claims to be a natural one, to afford at any rate a basis for the discussion of affinities." The only feature "open to criticism" upon which Dr. SCOTT lifts the veil is in regard to the absence of foliar gaps in Equisetum. His words are as follows: "The absence of foliar gaps, upon which JEFFREY lays stress, may hold good in the case of Archeocalamites, but if I rightly interpret the structure, they are present in the Calamariaceae as well as in the recent genus." It will be the writer's task to show that not only are foliar gaps absent in the older genera of the Equisetales, but that they also do not occur in the living genus Equisetum.

Professor CAMPBELL'S criticism of the present writer's work on

[11] Structure, development, and affinities of Equisetum. Boston Soc. Nat. Hist. Memoirs **5**: no. 5. p. 176.

Equisetum[12] carries less weight on account of his lack of first-hand familiarity with the extinct members of the Equisetales, a necessary basis for the discussion of a group which has its history so largely in the past. His first objection is that the vascular system of Equisetum is, on the basis of growing point development, of cortical origin and consequently cannot belong to the central cylinder, a term which in this case, according to Professor CAMPBELL, must be restricted to the pith, since it alone takes its origin from the sacrosanct region of the plerome. It is perhaps too late to discuss conclusions drawn from growing point morphology; they often lead rather to a *reductio ad absurdum* than to any useful or logical results. Professor BOWER has set a very good example in his recent book in throwing the growing point theory and the octant theory overboard.[13] Professor CAMPBELL sees no reason why there should be an attempt to reduce the vascular system of Equisetales to either of the types found in the other phyla of the pteridophytes. He further adds that the equisetal series presents resemblances which "indicate a real although extremely remote relationship with the lower ferns," thus committing the very error he previously condemned. Professor CAMPBELL also attaches a good deal of importance to the presence of multiciliate antherozoids as an indication of affinities, and regards this feature both in the Equisetales and Isoetaceae as indicative of filicinean affinities. His views in both instances are at variance with those of modern paleobotanists.

It will be well in our discussion of the Equisetales to begin with the living genus and thence go backward, for only in the living form is it possible to study the anatomical relations with necessary completeness. The reproductive axis of Equisetum will also afford a better starting-point than the vegetative, since it is a well-established principle of the new morphology that the reproductive structures are more likely to retain ancestral characters than the vegetative ones. *Fig. 3* shows a longitudinal section through one of the fibrovascular strands of the cone of *Equisetum telemateia*, at a region where a trace is being given off to a sporophyll. It will be noticed that the sporophyll trace passing off on the left of the figure goes outward and

[12] Affinities of the genus Equisetum. Amer. Nat. 39:273–285. 1905.

[13] Origin of a land flora, chaps. 14 and 42.

upward, without causing any break in the continuity of the fibro-vascular strand of the axis from which it is derived. On the inner side of the axial strand is to be seen a longitudinal space, the protoxylem lacuna. This is continuous through the nodal region in the cone, although in the vegetative axis, as will appear below, the lacuna is interrupted below each so-called zone of nodal wood. The condition of continuity through the nodal region presented by the protoxylem lacuna in the cone of Equisetum is paralleled by similar conditions described by WILLIAMSON in the nodal region of Calamites. *Fig. 2* represents a transverse section through the cone of the same species of Equisetum which makes clear the topography of the sporophyll trace and its corresponding axial strand as seen in this plane. There is no indication of any gap in the strand of the axis corresponding to the outgoing leaf-trace, which exactly subtends it. The examination of a large number of sections has convinced the author that foliar gaps do not in any case occur in the cone axis of Equisetum in connection with the passing-off of the traces of the sporophylls. The sporophyll trace is only about one-third to one-fourth the magnitude of the axial strand from which it arises, and consequently if any indication of a gap were present it would be clearly recognizable. *Fig. 1* shows a general view of a cross-section of the cone of *Equisetum telemateia*, indicating the relation of several sporophyll traces to their corresponding axial bundles. In the cone the foliar traces are vertically somewhat displaced on account of the crowded arrangement of the peltate sporophylls, so that even in accurately transverse sections all of them are not cut at the same level. On the left of the figure a trace has recently left its corresponding axial strand. The next foliar trace to the right is much farther out in the cortex than the first. The interval, corresponding to the next axial strand, does not show a trace, as this is not in the plane of section for the reason indicated above. In the case of the fourth trace the conditions are much as they are in the second; while the fifth trace is just leaving its axial strand. It will be seen by inspection of the whole figure that in each case where a sporophyll trace is present, it subtends the axial bundle from which it was derived in the lower part of its course. There is accordingly no foliar gap present. These micro-anatomical results only serve to confirm the

statement made by the author, in his memoir on Equisetum, concerning the frequent failure to alternate at the nodes, which is characteristic of the strobilar strands of that genus. This feature is illustrated photographically in *pl. 30, fig. 3,* of the memoir. The author's critics do not appear to have found this evidence sufficient. It is important to insist on the correspondence of the micro-anatomical absence of leaf gaps in the cone of Equisetum with the non-alternation of the axial strands of the cone at the nodes, because in some of the fossil forms we have only the latter evidence to go upon. It is perhaps a wise conservatism on the part of Dr. SCOTT to reject the evidence based on the frequent lack of alternation at the nodes, as seen in preparations of the bundle course in the cone of Equisetum. He can scarcely fail to be convinced by the microscopic demonstration of the absence of foliar gaps which has been given above and as represented in *figs. 1, 2,* and *3.* If it is reasonable to define a foliar gap as a gap in the wall of the stele, or one of its component strands in case the stele is not a continuous hollow cylinder, immediately above a leaf-trace, there are certainly no foliar gaps in the cone of Equisetum. The writer has satisfied himself that foliar gaps do not occur even when there is more or less complete alternation of the strands in the cone. *E. telemateia* has been chosen for illustration on account of the large size of the structures present. Similar results in every way are shown by *E. arvense* and *E. hiemale.*

It is now possible to turn with advantage to the examination of the outgoing foliar traces of the vegetative branches of Equisetum. As is well known, the internodal bundles of one segment of the stem in Equisetum alternate with those of the next, in this respect presenting a contrast to the condition of the strands in the cone and in the more ancient extinct genera of the phylum. The internodal strands of successive segments of the stem are joined in the region of the nodes by the so-called "nodal wood," which consists of a dense mass of short reticulated tracheids forming a completely closed ring. *Fig. 5* shows a longitudinal section through an outgoing leaf-trace and its corresponding cauline bundle. A large lacuna, the protoxylem cavity, is seen on the right of the axial strand. This disappears below the so-called "nodal wood." The outward course of the foliar trace is steeply upward, in contrast to that of the sporophyll

trace. Its tracheids obviously take their origin in the region of the protoxylem lacuna and below the "nodal wood." If the usual definition of a node be accepted, as marked by the outgoing leaf-traces, the so-called "nodal wood" of Equisetum in reality is above the node. *Fig. 4* shows a transverse section through a part of the "nodal wood" intervening between the bases of two branches. The leaf-trace lies just outside the mass of reticulated tracheids which compose the wood of the "node." It is obvious that there is no break in the mass of tracheids corresponding to the leaf-trace. Above the incorrectly designated "nodal wood" are the internodal bundles of the next segment of the stem, and between these are parenchymatous gaps, which on account of the alternation of the internodal bundles in different segments are above the leaf-traces, since the latter take their origin from the bundles of the lower internode. Professor CAMPBELL and Dr. SCOTT regard these as foliar gaps. They lack, however, one important feature of foliar gaps, for they do not occur *immediately above the traces*, as should be the case with true foliar gaps. All other foliar gaps with which we are acquainted show this feature. The *onus* of proving that the internodal lacunae of Equisetum are really foliar gaps appears consequently to lie upon the investigators who claim that they are to be regarded as such. It will be clear from the anatomical facts described above that in view of the relation of the leaf-traces to the so-called "nodal wood" it is quite incorrect to designate the ring of tracheids which lies *above* the outgoing leaf-traces as "nodal wood." It can only be called accurately supranodal wood. This distinction is a very important one to make, moreover, on phylogenetic grounds.

As a sequel to the description of the actual anatomical relations of the outgoing leaf-traces of the vegetative stem of Equisetum, it is natural to proceed to the discussion of the evolutionary or phylogenetic significance of the observed facts. The following citation from the memoir on Equisetum may appropriately be introduced at this point: "But STUR has shown that in the Ostrau beds, passing from the lower to the higher strata, a series of forms, *Calamites ramifer* Stur, *C. cistiformis* Stur, *C. approximatiformis* Stur, and *C. ostraviensis* Stur, represents transitions from the bundle arrangement of Archeocalamites, represented in *pl. 1, fig. 15*, to that of Equi-

setum, represented in *pl. 1, fig. 16*." It is obvious from the data of STUR, which have never been called in question, that the older Calamites were without the alternation of the strands in the region of the nodes which is characteristic of the more modern Calamites and the stem of the living Equisetum. It will be clear from the description of the anatomical conditions present in the cone of Equisetum that absence of alternation brings with it the complete absence of foliar gaps. The writer in his memoir has suggested that the explanation of the peculiar features of the foliar traces in the vegetative stem of Equisetum is to be found in the past history of the phylum to which it belongs. Dr. SCOTT would probably agree to the soundness of this proposition, for example, in the case of the older living gymnosperms. There appears to be no reason to make an exception in a group which has at least so long a past as the Gymnospermae. In the non-alternating arrangement of the internodal strands, characteristic of the stems of the older Calamites (which is still largely represented in the cone axis of the living genus), there were no foliar gaps immediately above the outgoing foliar traces. As the relations of the internodal strands of one internode to those of the next became changed in the progression from the archeocalamital to the equisetal mode of arrangement, the leaf-traces naturally came to lie opposite the gaps between the internodal strands of the next higher segment of the stem. But with the conservatism which is one of the most interesting characters of leaf-traces in general, they retained in Equisetum their old anatomical relations to the central cylinder of the stem. That is, they still pass off in the vegetative stem of Equisetum without leaving any true foliar gaps. The lacunae in the internodes cannot be regarded as foliar gaps, since they are not *immediately* above the foliar traces, but are separated from them by the depth of the so-called "nodal" wood! The explanation offered is a reasonable one in view of the past history of the group, and on those who do not accept it is placed the burden of some other more reasonable elucidation of the peculiar anatomical relations of the leaf-traces in the genus Equisetum.

The writer is credibly informed that Dr. SCOTT is of the opinion that the internodal gaps in the genus under discussion are *de facto* foliar gaps. This is a somewhat surprising opinion on the part of

one whose brilliant investigations on the anatomy of the cycadean peduncle have put the whole subject of the affinities of the cycads with the lower extinct gymnosperms in a new light. Dr. SCOTT from his discovery of centripetal xylem in the peduncles of the reproductive axes of certain living cycads reached the conclusion that their ancestors with strong probability possessed similar bundles in their vegetative stem. This condition is in fact realized in certain of the Pteridospermeae, particularly in Lyginodendron, which Dr. SCOTT regards as a probable ancestor of the cycads. There can be no question that Archeocalamites and Calamites are very much more nearly related to Equisetum than is Lygindodendron or any similar form to the living cycads. It follows that the reproductive axis of Equisetum is much more likely to perpetuate the ancestral characters of its stock than is the cycadean cone. It appears to have been shown above beyond any doubt that the equisetaceous strobilus perpetuates both the non-alternating strands and the complete absence of foliar gaps of the oldest calamitean forms. In the light of these facts there can be no reasonable doubt that the peculiar anatomical relations of the vegetative foliar traces of Equisetum are likewise persistently retained indications of the ancestral condition, for although the shifting of the internodal strands in the course of evolution has caused them to subtend the gaps between the strands of the next upper internodes, they still leave the central cylinder without giving rise to true foliar lacunae, and are moreover separated from their apparent gaps by the whole depth of the supranodal wood. Collateral evidence of the correctness of this view of an even more cogent kind has been discovered, but is reserved for a subsequent communication.

The older members of the equisetal alliance may now be considered. WEISS in one of his superb and classic monographs on the Carboniferous Calamites[14] has published a number of illustrations of calamitean cones. On *pls. 1* and *2* are figures of the genus Stachannularia, which show clearly the phenomenon of non-alternation at the nodes of the cone. *Pls. 3* and *4* show the same phenomenon in the well-known genus Calamostachys. In *pl. 9* a similar condi-

[14] Steinhohlen-Calimarien. Atlas zu denAbhandlungen Gelog. Specialkarte V. Preussen 2[1]: Berlin. 1871.

tion is figured in the cones of the remarkable genus Cingularia. Our information on the subject of the strobilus of the important calamitean genus Palaeostachya has recently been materially increased by the important investigations of HICKLING.[15] This author states: "From an examination of the numerous sections cut more or less transversely through the node, I feel little doubt that no regular pectination occurred; while on the other hand one or two sections showed features which seemed explicable only on the assumption that an occasional communication (probably irregular) did occur between adjacent bundles." The conditions in this genus of calamitean cone would seem accordingly to have approximated very closely those existing in the strobilus of the modern Equisetum, so far as the course of the bundles in relation to the nodes was concerned. This resemblance is all the more striking because, lower down on the same page, the author states that the sporophyll trace left the axial strand without giving rise to any foliar gap. His words are "*no gap is left in the main bundle.*" The italics are those of the present writer. "The main bundle" here means the bundle of the axis from which the sporophyll trace was derived. It will be readily inferred from the various citations given above that, in spite of the conviction expressed by Dr. SCOTT that foliar gaps occurred in the vegetative stem of the Calamites, they must have been generally absent in the cones of the more important calamitean types. There seems accordingly little reason to doubt, when the foliar relations of the more modern Calamites are fully worked out, since the course of their internodal strands resembled that found in Equisetum, that they will prove to be very similar to those of the living genus; and, in view of the similarity shown above in the fibrovascular arrangements of the cone, will be susceptible of a similar interpretation. This follows all the more certainly because so distinguished an authority as Dr. SCOTT himself states, in his *Studies in fossil botany:* "Thus the calamite, so far as anatomy goes, is simply an Equisetum with secondary thickening."

The conditions in Archeocalamites, the oldest calamitean genus, are particularly significant. In this form one of the most characteristic features was the failure of the primary fibrovascular strands of the vegetative stem to alternate at the nodes, as they do in the more

[15] Anatomy of *Palaeostachya vera.* Annals of Botany **21**:375. 1908.

modern Calamites and in Equisetum. It follows that there could have been no foliar gaps in this genus, if the general anatomical conditions were like those found in the rest of the calamitean stock, as has already been indicated by the present writer in the memoir on Equisetum. Our knowledge of the cone of Archeocalamites is very incomplete and nothing is known of its anatomical structure.

It may be stated with some confidence, if credence is to be attached to the doctrine of descent and to the general principles of modern plant anatomy, that the equisetal stock entirely lacks foliar gaps immediately above the outgoing leaf-traces. Dr. SCOTT'S statement that in respect to their vascular anatomy the Equisetales "reach the level of the simpler gymnosperms or dicotyledons" (*Progressus rei botanicae*, p. 157) will apparently, as a consequence, need some revision. There further seems to be no reason to doubt that the Equisetales are quite typical Lycopsida in the sense defined in the writer's two memoirs, and are as a consequence far removed from any mere affinity with any of the pteropsid series.

It may be added that there seems to be no reason at the present time, on anatomical grounds at any rate, to suppose that the Pteropsida had a sphenophylloid or ophioglossaceous origin from the Lycopsida. Neither Pseudobornia, of the reproductive organs of which we know little and of the anatomical structure of which we are entirely ignorant, nor Ophioglossum, of which the characters anatomical and reproductive are entirely filicinean, can serve as a phylogenetic link between the primitively small-leaved ventrisporangiate (adaxial) forms (Lycopsida) and the palingenetically large-leaved dorsisporangiate (abaxial) forms (Pteropsida). As Professor TANSLEY has recently put it in a review of Professor BOWER'S *Origin of a land flora*,[16] "on the general point of the relation of the 'microphyll' to the 'megaphyll,' there is no evidence of any capacity of the microphyll to evolve the megaphyll."

Summary

1. True foliar gaps occur *immediately above* their corresponding leaf-traces and are not *lateral* to the leaf-traces.

2. Foliar gaps are absent in Phylloglossum, although a super-

[16] New Phytologist 7:125. 1908.

ficial examination of the anatomy of this genus might lead to the conclusion that the perforations in the tubular stele, which are sometimes *lateral* to the outgoing leaf-traces, are to be regarded as true foliar lacunae.

3. Foliar gaps are likewise absent in Tmesipteris, and recent statements as to their presence are based on misinterpretation or misconception. Perforations in the stele are here also found sometimes *lateral* to one or *more* leaf-traces, but these cannot be regarded as true foliar gaps.

4. Foliar gaps are absent in the Lepidodendreae and the Sigillariae, but in the more modern species of the latter perforations of the tubular central cylinder are sometimes found, which have the same relations and are susceptible of the same explanation as are the similar perforations in Phylloglossum and Tmesipteris.

5. Foliar gaps are unquestionably absent in the cone axis of Equisetum, and on the basis of comparative anatomy are absent also in the vegetative stem. Similar statements apply to the reproductive and vegetative axes of Calamites. Archeocalamites has no foliar gaps in its vegetative stem.

6. The Lycopsida as defined by the author are clearly marked off from other plants by a palingenetically microphyllous habit, the absence of foliar gaps in the tubular stele, and by the possession of sporophylls with adaxial sporangia. They constitute a great natural phylum.

In conclusion the writer wishes to express his thanks to Miss SYKES, Professor A. A. LAWSON, Professor G. J. PIERCE, Dr. HOLMAN (Stanford University), and Mr. L. A. BOODLE for material which they have kindly put at his disposal.

HARVARD UNIVERSITY

EXPLANATION OF PLATES

PLATE XVII

FIG. 1.—Transverse section of part of the cone of *Equisetum telemateia*. ×15.

FIG. 2.—Transverse section showing the axial bundle and its outgoing foliar trace of the cone of *E. telemateia*. ×25.

FIG. 3.—Longitudinal section of the same. ×25.

FIG. 4.—Transverse section through the supranodal wood of the vegetative

axis of the same species of Equisetum, showing the absence of a foliar gap corresponding to the leaf-trace which lies in the cortex. ×25.

FIG. 5.—Longitudinal section through a vegetative node of the same species of Equisetum, showing the departure of the leaf-trace without causing any gap in the supranodal wood. ×25.

PLATE XVIII

FIG. 6.—Transverse section of the stem of *Tmesipteris tannensis*. ×15.

FIG. 7.—Tranverse section of the same, showing the relation of the outgoing traces to the central cylinder. ×30.

FIG. 8.—Copy of a figure from BERTRAND, showing the departure of the traces of the lower sporophylls from the upper region of the peduncular strands in Phylloglossum.

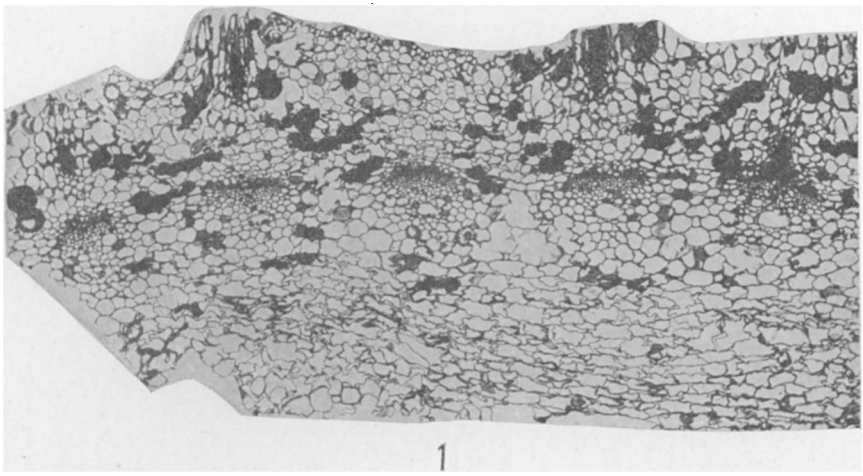
FIG. 9.—Transverse section of part of the central cylinder of *Lepidophloios Harcourti*.

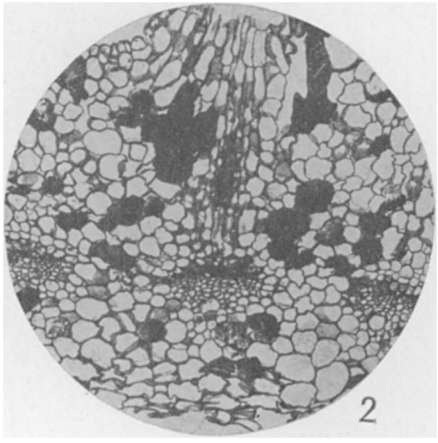
FIG. 10.—Transverse section through the middle region of the cone in Phylloglossum, showing the relation of the leaf traces to the central cylinder. ×60.

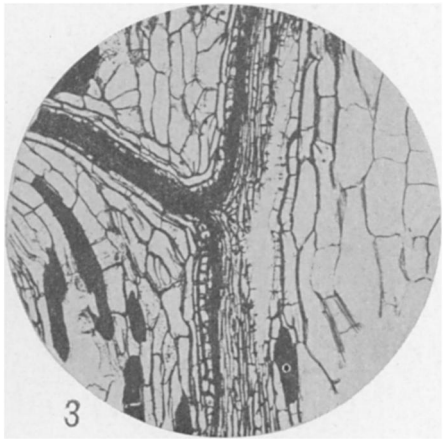
FIG. 11.—Transverse section through the central region of the cone in another example of Phylloglossum, showing two apparent "foliar gaps." ×60.

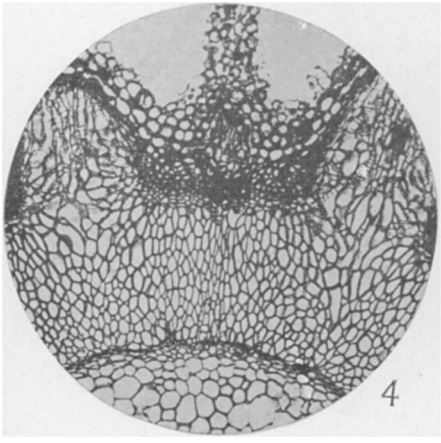
FIG. 12.—Transverse section through the same cone slightly lower down, showing the connection of the foliar strand with the side of the apparent foliar gap. ×60.

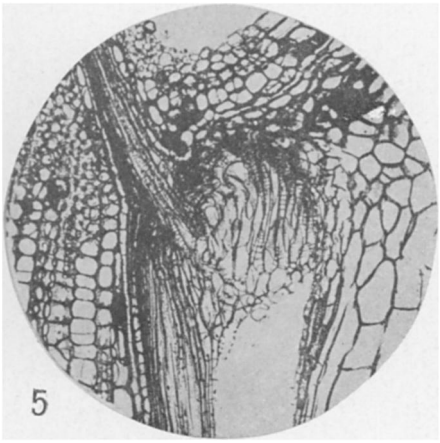
NOTE.—*Figs. 10, 11, 12* are all made from herbarium specimens. In *fig. 12* the action of caustic alkali has not quite restored the size of the cells in the gap on the right of the central cylinder; it should appear the same size as that shown on the right of *fig. 11*.



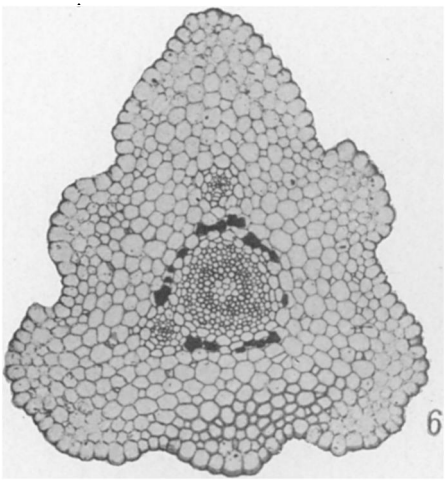


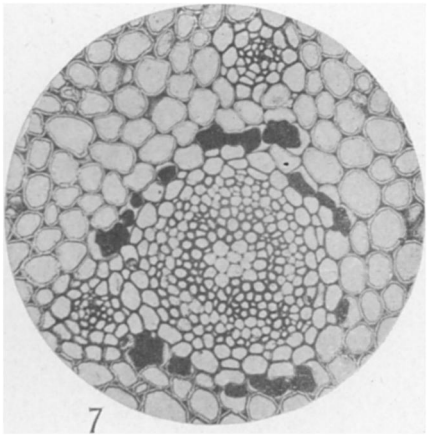


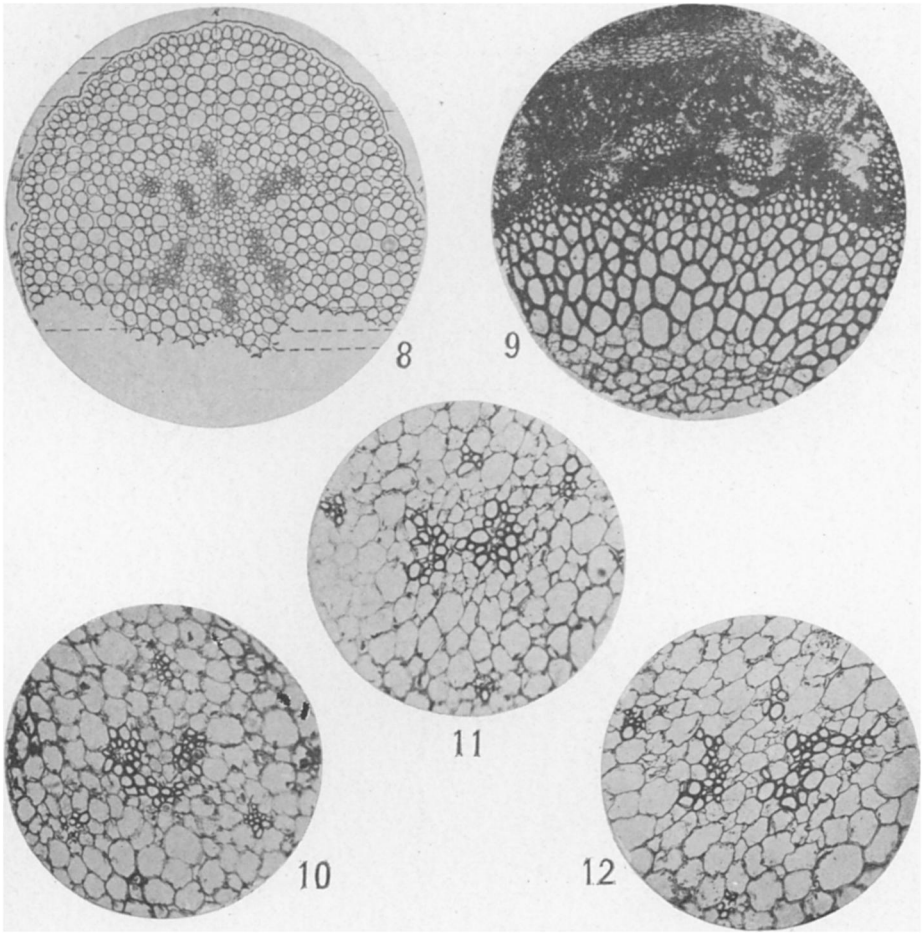




JEFFREY on LYCOPSIDA







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